## Horizontal Gene Transfer and Microbial Evolution: Is the "Tree of Life" a Tree?

## J. Peter Gogarten

Department of Molecular and Cell Biology, University of Connecticut, Storrs, CT, USA

Tree-like binary schemes for taxonomic classification have an illustrious history in evolutionary biology, but they do not provide a complete representation of life's history, especially for prokaryotes[1]. All functional categories of genes are susceptible to horizontal gene transfer, including ribosomal rRNA operons and genes associated with phylum-defining characteristics such as the photosynthetic machinery[2].

We continue to develop tools that extract phylogenetic information from completely sequenced prokaryotic genomes without assuming a shared evolutionary history for the different gene families (e.g., [3-6]. Spectral analyses of either all possible bipartitions and of all possible embedded quartets for sets of orthologous genes allow to recognize and extract the consensus phylogeny that is supported by the plurality of orthologous sets, and to detect those genes that conflict with this plurality consensus. Quartet-based spectra allow us to identify quartets that are poorly supported across all sets of orthologous genes. Datasets conflicting with these often poorly resolved quartets could be false positives candidates for horizontal gene transfer. Overall poorly supported quartets are eliminated from further analyses.

Not all genes are equally itinerant. Some clearly have a higher propensity for transfer than others, and not all groups of organisms experience horizontal gene transfer to the same extent. The organismal line of descent for many microbial species contains only a small core of genes that is very similar for all members of the species, and even the genes in this core can be exchanged between divergent species, but instances of these exchanges are only rarely detected. The more conserved core is surrounded by a vapor of genes, which sometimes reside in the genomes, but most of the time these genes are found in extra-chromosomal elements (phages and plasmids) (cf. [1]).

Over long periods of time gene transfer makes organisms existing in the same environment more similar to one another. This is most clearly seen in case of organisms that live in environments that are otherwise inhabited by distant relatives only. Methods of phylogenetic reconstruction that explicitly allow for reticulation events promise a more realistic reconstruction of much of life's history. In particular, reticulation events allow correlating evolutionary events in different parts of the "tree-of-life"[7].

- 1. Gogarten, J.P. and J.P. Townsend, *Horizontal gene transfer, genome innovation and evolution*. Nat Rev Microbiol, 2005. **3**(9): p. 679-87.
- 2. Gogarten, J.P., W.F. Doolittle, and J.G. Lawrence, *Prokaryotic evolution in light of gene transfer*. Mol Biol Evol, 2002. **19**(12): p. 2226-38.
- 3. Zhaxybayeva, O. and J.P. Gogarten, *Bootstrap, Bayesian probability and maximum likelihood mapping: Exploring new tools for comparative genome analyses.* BMC Genomics, 2002. **3**: p. 4.
- 4. Zhaxybayeva, O. and J.P. Gogarten, *An improved probability mapping approach to assess genome mosaicism.* BMC Genomics, 2003. **4**(1): p. 37.
- 5. Zhaxybayeva, O., P. Lapierre, and J.P. Gogarten, *Genome mosaicism and organismal lineages*. Trends Genet, 2004. **20**(5): p. 254-60.
- 6. Hamel, L., O. Zhaxybayeva, and J.P. Gogarten, *PentaPlot: A software tool for the illustration of genome mosaicism*. BMC Bioinformatics, 2005. **6**(1): p. 139.
- 7. Huang, J., Y. Xu, and J.P. Gogarten, *The Presence of a Haloarchaeal Type Tyrosyl tRNA Synthetase Marks the Opisthokonts as Monophyletic.* Mol Biol Evol, 2005.